NeoBiota 84: 137–167 (2023)
doi: 10.3897/neobiota.84.95864
https://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Pining away and at home: global utilisation of *Pinus radiata* by native and non-native insects*

Eckehard G. Brockerhoff[1], Belinda A. Gresham[2], Nicolas Meurisse[2], Helen F. Nahrung[3], Anouchka Perret-Gentil[1], Andrew R. Pugh[2], Stephanie L. Sopow[2]**, Rebecca M. Turner[4]**

1 *Swiss Federal Research Institute WSL, Birmensdorf, Switzerland* **2** *Scion (New Zealand Forest Research Institute), Rotorua, New Zealand* **3** *Forest Research Institute, University of the Sunshine Coast, Sippy Downs, Queensland, Australia* **4** *Scion (New Zealand Forest Research Institute), Christchurch, New Zealand*

Corresponding authors: Eckehard G. Brockerhoff (eckehard.brockerhoff@wsl.ch);
Stephanie L. Sopow (stephanie.sopow@scionresearch.com)

Academic editor: M. Branco | Received 1 October 2022 | Accepted 7 February 2023 | Published 18 May 2023

Citation: Brockerhoff EG, Gresham BA, Meurisse N, Nahrung HF, Perret-Gentil A, Pugh AR, Sopow SL, Turner RM (2023) Pining away and at home: global utilisation of *Pinus radiata* by native and non-native insects. In: Jactel H, Orazio C, Robinet C, Douma JC, Santini A, Battisti A, Branco M, Seehausen L, Kenis M (Eds) Conceptual and technical innovations to better manage invasions of alien pests and pathogens in forests. NeoBiota 84: 137–167. https://doi.org/10.3897/neobiota.84.95864

Abstract

Pinus radiata (radiata pine or Monterey pine) is threatened in its native range in California and, at the same time, one of the most widely-planted tree species worldwide, especially in the southern hemisphere. It is affected by a wide range of plant-feeding insects both in its native range and in regions where it is planted as an introduced tree. In addition, there are many invasive insects that have colonised *P. radiata*, in some cases causing major damage. Here, our objectives were to provide a complete and up-to-date overview of all insect species recorded from *P. radiata* worldwide, to summarise where these insects are native and which countries or regions they have invaded, to categorise them according to their impacts as damaging species or as vectors of plant pathogens, and to examine border interceptions to determine whether pathways exist that would allow these species to enter and potentially invade additional regions. Our compilation of insects feeding on *P. radiata* provides a list of 649 species (and an additional 11 species identified at the genus level only). Coleoptera is the most represented order in the list (299 species), followed by Lepidoptera (224 species) and Hemiptera (65 species). We classified 28 species as high-impact, including 12 true bark beetles (Coleoptera: Curculionidae: Scolytinae), eight Lepidoptera, five other Coleoptera,

* This paper is dedicated to the late John Bain, eminent forest entomologist at the New Zealand Forest Research Institute, who devoted much of his career to studying insects on *Pinus radiata*.

** Joint last authors who contributed equally.

two Hymenoptera and one Hemiptera. These species can cause substantial direct damage or act as vectors of highly-damaging plant pathogens. Other species cause only occasional damage, rarely requiring management (classified as 'low-medium impact') or they are generally benign ('negligible impact'). Hemiptera and Scolytinae have a high proportion of species established outside their native range. The Nearctic and Neotropic regions have been invaded by the most high-impact species, mainly by species native to Europe. Border interceptions of 185 species (29% of those on our list) were recorded during import inspections between 1995–2021, indicating considerable potential for further invasions. The findings of our study can be used to identify potential high-impact invaders and the pathways that may require more phytosanitary attention. Furthermore, our analyses provide useful insights into the insect-plant interactions resulting from the global distribution of a tree species and the native and non-native insects feeding on it.

Keywords
Biological invasions, establishment, impact assessment, insect herbivores, interceptions, Monterey pine, pest risk analysis, Pinaceae, plantation forest, radiata pine

Introduction

Pinus radiata D. Don (Monterey pine or radiata pine) is one of the most extensively-planted tree species worldwide (Lavery and Mead 1998; Mead 2013). Although the native area of *Pinus radiata* is less than 6000 ha in coastal California and islands off the coast of Baja California, its fast growth rate, usefulness for a wide range of purposes, and suitability across a range of temperate climatic conditions, have led to it being a preferred choice for plantation forestry, especially in the southern hemisphere (Lavery and Mead 1998). It is planted on a large scale as an introduced (non-native) species mainly in Chile (ca. 1.9 million ha (CONAF 2021)), New Zealand (ca. 1.5 million ha (NZFOA 2021)), Australia (ca. 0.7 million ha (Legg et al. 2021)) and South Africa (ca. 40,000 ha (Forestry Economics Services CC 2020), but formerly ca. 0.1 million ha (Lavery and Mead 1998)). In addition, it has been planted in Spain (0.2 million ha (Mead 2013)) and in other European countries including Italy and France (CABI 2019, Mead 2013), as well as in China (e.g., Bi et al. 2003, 2013) and, to a lesser extent, in several other countries (CABI 2019).

Given the importance of *P. radiata* for forestry, there is considerable interest in insects and pathogens affecting tree health. In its native range, *P. radiata* suffers from a number of important insect pests (e.g., Ohmart 1982a) and pathogens (Gordon et al. 2001). In other parts of the northern hemisphere where other pine species are native, the introduced *P. radiata* is severely affected by native pests of pines (e.g., Cobos-Suarez and Ruiz-Urrestarazu 1990, Castedo-Dorado et al. 2016). By contrast, in the planted areas in the southern hemisphere, its pest burden is comparatively low because the lack of native pines or other Pinaceae south of the equator means there are few native insects that cause substantial damage to pines (e.g., White 1974; Berndt et al. 2004; Wingfield et al. 2008a). Non-native plants without close relatives in their introduced range are usually less affected by native phytophagous insects than those with close relatives in the native flora (e.g., Harvey et al. 2012; Branco et al. 2015). Therefore, pine planta-

tions planted well outside the native range of pines in the southern hemisphere were in a largely enemy-free space, consistent with the enemy-release hypothesis (Mitchell and Power 2003; Colautti et al. 2004). However, these pine plantations are highly susceptible to invasion by insect pests left behind in their native range (i.e., reconnection of "old associations"), pine pests from other regions, and by polyphagous insects and those feeding on closely related plants in their introduced range (i.e., "new associations"). The risk of invasions is confirmed by the steady increase in the number of established non-native insects that affect plantations of non-native pines and other trees (e.g., Hurley et al. 2016; Brockerhoff and Liebhold 2017; Nahrung and Carnegie 2020).

The arrival of highly damaging non-native pests in southern hemisphere plantations of *P. radiata* began with the woodwasp *Sirex noctilio* which was detected in New Zealand in 1900 (Bain et al. 2012) and subsequently invaded most southern hemisphere regions where pines are grown (Slippers et al. 2015). Other notable invasive insect pests of *P. radiata* are the eastern five-spined engraver bark beetle (*Ips grandicollis*) first recorded in Australia in the 1940s (Neumann 1987), the European pine shoot moth (*Rhyacionia buoliana*) first found in Chile in 1985 (Alvarez and Ramirez 1989), and the Monterey pine aphid (*Essigella californica*) detected in Europe, Australia, New Zealand and South America between the 1980s and early 2000s (Watson et al. 2008; Eyles et al. 2011). However, most of the more damaging insect species feeding on *P. radiata* still have a limited distribution and many have not yet invaded the southern hemisphere countries with large *P. radiata* plantations. Consequently, there was and is much interest in risk assessments and surveys for insect pests of *P. radiata* to identify potential invaders and to prevent their invasion (e.g., Allen 1973; Ohmart 1980; Carter and Griffith 1989; Mead 2013; Brockerhoff and Bulman 2014; Brockerhoff et al. 2016; Lawson et al. 2018). However, there has not been a comprehensive assessment of the insects feeding on *P. radiata* since the 1980s when Clifford P. Ohmart studied insects associated with it in its native region and all main areas where it was planted (Ohmart 1980, 1982a, b). In addition, the role of insects as vectors of pathogens has received more consideration since then (e.g., Hoover et al. 1996; Kirisits 2004; Wingfield et al. 2008a).

The objectives of the present study are:

(1) to provide a complete and up-to-date overview of all insect species recorded from *P. radiata* in its native and introduced ranges,

(2) to summarise where these insects are native and which countries or regions they have invaded,

(3) to categorise these species according to their impacts as damaging species or as vectors of plant pathogens,

(4) to examine whether border interceptions have been recorded, which would indicate that pathways exist that would allow these species to enter and potentially invade additional regions, and

(5) to provide additional information on these points specific to New Zealand and Australia because more detailed records and data are available for these countries.

Methods

Sources of insect records from *Pinus radiata*

We compiled world-wide records of insect species recorded on *Pinus radiata* that incorporated the original lists of Ohmart (1980, 1981, 1982a, b) and additional records from New Zealand and other countries which had been continuously added to and curated by John Bain (Scion (New Zealand Forest Research Institute)). Beginning in 2018, this list was thoroughly reviewed and updated with a literature search using the Scopus database (see below) as well as forward and backward searches in relevant publications. In 2020, a list independently compiled by Helen Nahrung (University of the Sunshine Coast, Queensland, Australia) with records from Australia was incorporated. Additional records were added between 2020 and 2022 by further interrogating the literature, Scion's Forest Health Database and other available databases. The main criterion for inclusion in our pine pest list was that species feed on any tissue of *P. radiata* (see below for more information on the impact classification). The full species list with references is available as Suppl. material 1: table S1 and at the online repository Zenodo (Brockerhoff et al. 2023).

Taxonomy and geographic distribution

Using the scientific name of each insect as the search term, the current taxonomy, synonyms and distribution in native and introduced ranges were retrieved for all species, initially by systematic searches using Scopus (https://www.scopus.com), Google Scholar (https://scholar.google.com), the CABI Invasive Species Compendium (https://www.cabi.org/ISC), the Global Biodiversity Information Facility (GBIF, https://www.gbif.org), NZOR – New Zealand Organisms Register (https://www.nzor.org.nz), the Atlas of Living Australia (https://www.ala.org.au), the Australian Faunal Directory (https://biodiversity.org.au/afd/home), and the Australian Plant Pest Database (https://www.appd.net.au) as well as Google (https://www.google.com) and Wikipedia (https://en.wikipedia.org). Other databases (some taxon-specific) and literature records were accessed as required, and in some cases, experts were consulted directly (see references in Suppl. material 1: table S1). Establishment data were cross-checked against the 'International non-native insect establishment data' database (Turner et al. 2021b).

The species list was standardised taxonomically using the GBIF taxonomic database (GBIF Secretariat 2021) and the "taxize" package in R (Chamberlain and Szöcs 2013). For any names not recognised by GBIF, standardisation was performed manually via searches of other databases and literature. Coleoptera family names were based on the framework in Bouchard et al. (2011), and Lepidoptera families as per Mally et al. (2022).

For each species, native and non-native occurrences were grouped by biogeographic regions defined as shown below. Our biogeographic regions are mostly aligned with those of Udvardy (1975) but not strictly because our information sources were specific

to countries of occurrence, whereas the borders of Udvardy's biogeographic realms often pass through countries (i.e., one country can be in more than one region).

Our regions are defined as follows:

- Western Palearctic ("W Palearctic"): Europe, North Africa and Near East;
- Eastern Palearctic ("E Palearctic"): Northern and eastern Asia and including the Indo-Malayan region;
- South West Pacific ("SW Pacific"): Australasia and Pacific Islands (excluding Hawaii);
- Afrotropic: Sub-Saharan Africa;
- Nearctic: North America including all of Mexico and Hawaii;
- Neotropic: South and Central America (excluding all of Mexico) and the Caribbean.

Using the information on occurrences of native species and establishments of non-native species, we compiled for each biogeographic region (i) the number of native species feeding on *P. radiata*, (ii) the number of established non-native species feeding on *P. radiata*, and (iii) the number of species originating from each region that became established in another region or in another country in the same region.

Interception data

Three datasets with border interceptions were analysed to determine which of the species on our list have been intercepted during border inspections of imports, vessels and containers, and in some cases international mail and passenger baggage. Post-border interceptions were not considered.

Unless otherwise stated, analyses with border interception data were conducted using an international dataset. This recent dataset is a collection of international border interceptions between 1995 and 2021 in New Zealand, Australia, South Africa, South Korea, Japan, Canada, the United States, the United Kingdom and the European and Mediterranean (EPPO) region. The international interception dataset is comprised of the border interceptions described in Turner et al. (2021a). In addition, we queried South African border interceptions from Saccaggi et al. (2021), additional border interceptions from Japan between 1996–2019 extracted from http://www.pps.go.jp/TokeiWWW/Pages/report/index.xhtml (Plant Protection Station, The Ministry of Agriculture, Forestry and Fisheries of Japan), and updated EPPO border interceptions for the 2011–2021 period from the Europhyt annual interception reports. Included in the international dataset was the New Zealand data subset which spans the period from 2000–2017 (Turner et al. 2021a) which was used for a country-specific analysis.

Additional statistics were drawn from two older border interception databases. Firstly, the Scion BUGS database for New Zealand 1950–2000 which contains border interceptions of species relevant for trees, and secondly the USDA 1949–2008 interceptions of Scolytinae and Cerambycidae (Brockerhoff et al. 2014).

Impact classification

Each species on the list was assigned one of three impact ratings relating to evidence of pest status on *P. radiata*: 'negligible impact' – species where no interventions, management or damage records were found; 'low-medium impact' – species with evidence of damage, management or control but this was either short-term, localised or minor; and 'high impact' – species that required ongoing management and/or had significant economic effects, such as severe damage to forest or amenity trees and/or are important vectors of highly damaging pathogens of *P. radiata*. Species causing severe impacts on human or veterinary health (e.g. from urticating hairs of caterpillars) were also considered 'high impact'. In some cases, we combined species in the low-medium and high impact categories as species of 'non-negligible impact'. Impacts related to market access were excluded in our study because these are often associated with species that do not damage live trees or cause no damage at all. Likewise, impacts of species whose recorded damage was exclusive to timber in service, such as borers in dry deadwood, were excluded because the focus of our assessment was on insects feeding on living trees. Consequently, species exclusively affecting market access or causing only damage to timber in service were classified as having negligible impact.

Our impact classification differs from the now widely used EICAT classification (IUCN 2020) because our impacts relate mainly to damage to *Pinus radiata* planted for commercial purposes outside their native range and in some cases also to trees in their native range, whereas EICAT focuses only on "impact to native taxa" (IUCN 2020, p. 8). However, our categories can be translated to approximately corresponding EICAT categories ('negligible impact' = 'minimal concern'; 'low-medium' = 'minor'; 'high impact' = 'moderate'). None of the insects considered in our list have a 'major' or 'massive' impact according to EICAT as both these involve at least local extinction of the affected species.

Analyses

The final dataset containing all insect species feeding on *Pinus radiata* was analysed and visualised in R version 4.1.2 (2022-05-20). When analysing by biogeographic region, we excluded seven cosmopolitan species with a widespread distribution across multiple biogeographic regions where it could not be determined which regions were part of the native or non-native range. When analysing non-native species, we included species which were successfully eradicated as these represent the establishment potential in the absence of a post-border biosecurity response. For example, four of the species invasive to New Zealand fell into this category (*Coptotermes acinaciformis*, *Coptotermes frenchi*, *Cryptotermes brevis* and *Teia anartoides*).

Comparisons were made among all insects on the pine pest list (i.e., any species feeding on *Pinus radiata*) as well as specifically among the "non-negligible" impact species (those in the combined low-medium or high impact categories).

To investigate relationships between border interceptions and establishments, the number of species was compared by taxon groups which were defined at the

level of insect orders with the exception of four particularly species-rich and important families/subfamilies (Cerambycidae, Scolytinae, Geometridae and Tortricidae) which were analysed separately. If relationships between interceptions and establishments were independent of taxon group, we would expect the number of established species in each group to be relative to the number of intercepted species in each group and proportional to the ratio of established insect species per intercepted insect species (i.e. expected number of establishments in taxa group = (total number of established insects)/(total number of intercepted insects)*(number of intercepted insects in taxa group). We assume that the number of established species per group can then be described by a Poisson distribution and calculate a prediction interval for each of our taxa groups. The prediction interval bounds were calculated to show the region within which all 11 taxa groups would be expected to fall 95% of the time. When calculating the interval quantiles, a Bonferroni correction was used for multiple comparisons.

The relationship between the number of native and non-native insects per biogeographic region was visualised on a scatter plot. The effect of feeding guilds (i.e., borers, defoliators, sap-feeders and others) was visualised by adding ellipses showing the 95% confidence intervals for a multivariate t-distribution (Fox and Weisberg 2011).

Pearson's chi-square test was used to test for evidence of differences in proportions between groups (i.e., negligible vs non-negligible, intercepted vs not intercepted, feeding guilds), followed by pairwise comparisons of proportions using the Holm (1979) method of adjustment for multiple comparisons. In situations where expected counts were fewer than 5, Fisher's exact test was used instead.

Results

Species recorded on *Pinus radiata*

We found records of 649 insect species (in 438 genera, 83 families and nine orders) feeding on *P. radiata* (Table 1, Suppl. material 1: table S1). An additional 11 records were named at the genus level only; these were all of negligible or low impact, and as their identity could not be confirmed, they were excluded from the analyses (but are listed in Suppl. material 1: table S1). Coleoptera is the most represented order (299 species or nearly 50% of all species), followed by Lepidoptera (224 species), Hemiptera (65 species), Blattodea (i.e., termites), Hymenoptera and other orders. Twenty-eight species were categorised as 'high impact' and 168 species as 'low-medium impact' (Table 1). The remaining 453 species (nearly 70% of the species total) were considered to have negligible impacts on *P. radiata* as no records of damage were found for these species (Table 1). Of the 49 insects on our list that are known to vector diseases, evidence of detrimental impact exists for 37 species. In terms of feeding guilds, most species are either borers or defoliators while sap-feeders and other guilds such as root feeders and cone insects are less represented (Table 2).

Table 1. Overview of pine pest list species, their impact classification, interceptions and establishments, grouped by main taxa. Note: Interceptions are based on the 1995-2021 international dataset (see methods). Establishments include species established unintentionally anywhere outside their native range around the world, regardless of whether or not they were subsequently eradicated, and include cosmopolitan species. See Fig. 2 for results of statistical tests comparing proportions among taxa for establishments and interceptions. Taxa with shared letters within a column were not significantly different in terms of the proportions within the column based on a Fisher pairwise test with Holm adjustment for multiple comparisons.

Taxa	Number of species in taxon	Number (percent) high impact*	Number (percent) low-medium impact*	Number (percent) negligible impact*	Number (percent) established	Number (percent) intercepted
Blattodea: Isoptera	22	0 (0) ab	3 (14) ab	19 (86) abc	9 (41) abc	6 (27) abcd
Coleoptera: Cerambycidae	69	1 (1) b	8 (12) b	60 (87) a	14 (20) bc	20 (29) bcd
Coleoptera: Curculionidae: Scolytinae	55	12 (22) a	16 (29) ab	27 (49) bc	20 (36) ab	35 (64) a
Coleoptera: Curculionidae: other	90	3 (3) ab	20 (22) ab	67 (74) abc	15 (17) bc	17 (19) cd
Coleoptera: other	85	1 (1) b	17 (20) ab	67 (79) ab	13 (15) bc	22 (26) bcd
Hemiptera	65	1 (2) b	16 (25) ab	48 (74) abc	36 (55) a	32 (49) ab
Hymenoptera	14	2 (14) ab	6 (43) ab	6 (43) bc	4 (29) abc	3 (21) abcd
Lepidoptera: Geometridae	40	0 (0) ab	9 (22) ab	31 (78) abc	3 (8) bc	2 (5) d
Lepidoptera: Tortricidae	33	2 (6) ab	17 (52) a	14 (42) c	6 (18) bc	11 (33) abcd
Lepidoptera: other	151	6 (4) b	46 (30) ab	99 (66) abc	19 (13) c	25 (17) d
All other orders	25	0 (0) ab	10 (40) ab	15 (60) abc	7 (28) abc	12 (48) abc
Total	**649**	**28 (4)**	**168 (26)**	**453 (70)**	**146 (22)**	**185 (29)**

*only impacts on living trees were considered.

Table 2. Pine pest list grouped by feeding type in terms of impacts, interceptions and establishments. Note: Impact is based on evidence for impact on *P. radiata*. Establishments included those of species established unintentionally anywhere outside their native range around the world inclusive of cosmopolitan species, regardless of whether or not they were subsequently eradicated. Interception data used here is the 1995-2021 international dataset (see methods). The letters in each column indicate the results from pairwise comparison of proportions with Holm adjustment for multiple comparison. Taxa with the same letters were not significantly different in terms of the proportions within the column. For detailed statistics, see Suppl. material 2: table S2.

Feeding guild	Number in feeding guild	Number (percent) high impact	Number (percent) low-mid impact	Number (percent) established	Number (percent) intercepted
Borer	270	20 (7)	48 (18) b	67 (25) b	87 (32) a
Defoliator	278	7 (3)	93 (33) a	31 (11) c	53 (19) b
Sap-feeder	67	1 (1)	17 (25) ab	37 (55) a	33 (49) a
Other	34	0 (0)	10 (29) ab	11 (32) ab	12 (35) ab
Total	**649**	**28 (4)**	**168 (26)**	**146 (22)**	**185 (29)**

High-impact species

The 28 species classified as high-impact comprised 17 Coleoptera (12 of which are true bark beetles (Scolytinae)), eight Lepidoptera, two Hymenoptera and one Hemiptera (Tables 1, 3). Twenty of these high-impact species are borers, seven are defoliators, and one is a sap-feeder (Table 3), with significant differences in proportions between groups (Table 2, Fisher's Exact Test, P=0.016). Seventeen of the 28 high-impact species are known vectors of serious pathogens affecting *P. radiata*, especially the pitch canker fungus *Fusarium circinatum* (Table 3). Other species are high-impact pests in their own right such as the European six-toothed bark beetle *Ips sexdentatus* which can occasionally cause substantial tree mortality.

Table 3. High-impact species feeding on *Pinus radiata*, their native and established regions, number of interceptions internationally, and important plant pathogens vectored (where applicable). Note that the East Palearctic includes records from the Indo-Malayan region.

Scientific name	Common name(s)	Feeding guild	Native region	Invaded regions	Interceptions	Vector of pathogens
Conophthorus radiatae Hopkins	Monterey pine cone beetle	Borer	Nearctic	–	0	*Fusarium circinatum*
Dioryctria sylvestrella (Ratzeburg)	New pine knot-horn, maritime pine borer	Defoliator	W Palearctic, E Palearctic	–	0	–
Ernobius punctulatus (LeConte)	–	Borer	Nearctic	–	4	*Fusarium circinatum*
Essigella californica (Essig)	Monterey pine aphid	Sap-feeder	Nearctic	W Palearctic, Neotropic, SW Pacific	0	–
Hyalarcta huebneri (Westwood)	Common leaf case moth	Defoliator	SW Pacific	–	0	–
Hylastes angustatus (Herbst)	–	Borer	W Palearctic	Afrotropic	1	*Fusarium circinatum*, *Leptographium procerum*
Hylastes ater (Paykull)	Black pine bark beetle	Borer	W Palearctic	Neotropic, SW Pacific	778	*Ophiostoma* spp., *Leptographium* spp.
Hylobius abietis (Linnaeus)	Large brown pine weevil, large pine weevil	Borer	W Palearctic, E Palearctic	–	11	–
Ips grandicollis (Eichhoff)	Eastern five-spined engraver, five-spined bark beetle, southern pine engraver	Borer	Nearctic	SW Pacific, E Palearctic	25	*Ophiostoma ips*
Ips mexicanus (Hopkins)	Monterey pine engraver	Borer	Nearctic, Neotropic	–	2	*Fusarium circinatum*
Ips paraconfusus Lanier	California five-spined Ips, California five-spined engraver	Borer	Nearctic	–	0	*Fusarium circinatum*
Ips plastographus maritimus (Lanier)	–	Borer	Nearctic	–	1	*Fusarium circinatum*
Ips sexdentatus (Boerner)	Six-toothed bark beetle	Borer	W Palearctic	–	453	*Fusarium circinatum*, *Leptographium* spp., *Ophiostoma* spp.
Lymantria dispar (Linnaeus)	Spongy moth, gypsy moth	Defoliator	W Palearctic, E Palearctic	Nearctic	465	–
Lymantria monacha (Linnaeus)	Black arches, nun moth	Defoliator	W Palearctic, E Palearctic	–	0	–
Monochamus galloprovincialis (Olivier)	Black pine sawyer beetle	Borer	W Palearctic	–	40	*Bursaphelenchus xylophilus*
Neodiprion sertifer (Geoffroy)	European pine sawfly, fox-coloured sawfly	Defoliator	W Palearctic, E Palearctic	Nearctic	1	–
Ormiscodes cinnamomea (Feisthamel)	–	Defoliator	Neotropic	–	0	–
Orthotomicus erosus (Wollaston)	Mediterranean pine beetle	Borer	W Palearctic, E Palearctic	Afrotropic, Nearctic, Neotropic	136	*Ophiostoma ips*, *Verticicladiella alacris*
Pissodes castaneus (De Geer)	Small banded pine weevil, banded pine weevil, lesser banded pine weevil	Borer	W Palearctic	Neotropic	3	*Leptographium* spp., *Armillaria* spp., *Sporothrix inflata*. Carrier but not confirmed vector of *F. circinatum*
Pissodes nemorensis Germar	Deodar weevil, northern pine weevil	Borer	Nearctic	Afrotropic	0	*Fusarium circinatum*, *Diplodia pinea*
Pityophthorus carmeli Swaine	–	Borer	Nearctic	–	0	*Fusarium circinatum*
Pityophthorus setosus Blackman	–	Borer	Nearctic	–	0	*Fusarium circinatum*
Rhyacionia buoliana (Denis & Schiffermuller)	European pine shoot moth	Borer	W Palearctic	Nearctic, Neotropic	0	–
Rhyacionia frustrana (Comstock)	Nantucket pine tip moth	Borer	Nearctic	–	0	–
Sirex noctilio Fabricius	Sirex woodwasp	Borer	W Palearctic, E Palearctic	Afrotropic, Nearctic, Neotropic, SW Pacific	29	*Amylostereum areolatum*
Thaumetopoea pityocampa (Denis & Schiffermuller)	Pine processionary moth	Defoliator	W Palearctic	–	0	–
Tomicus piniperda (Linnaeus)	Common pine shoot beetle, pine shoot beetle, larger European pine shoot beetle, larger pine shoot beetle	Borer	W Palearctic, E Palearctic	Nearctic	65	*Leptographium wingfieldii*, *Leptographium guttulatum*, *Ophiostoma minus*

Native species by biogeographic region

Seven cosmopolitan species which occur in multiple regions and for which the native range could not be determined were excluded from the analysis of native or invaded ranges except for the specific analysis for New Zealand and Australia (see below). Most native species feeding on *P. radiata* were recorded in the SW Pacific region (42% of all non-cosmopolitan species, with 167 species being native to Australia and 107 species native to New Zealand), followed by the Nearctic (20%), the Afrotropic (16%), the W Palearctic (12%) and the Neotropic region (12%) (Fig. 1A). The fewest native species feeding on *P. radiata* were recorded in the E Palearctic (6%). Despite the large number of species recorded for the SW Pacific, this region has just one native high-impact species (the Australian psychid moth *Hyalarcta huebneri* (Table 3)). The three southern hemisphere regions have the highest proportions of species with negligible impact and an average proportion of low-medium impact species (Fig. 1A). The W Palearctic has a high proportion and the largest number of high-impact species recorded on *P. radiata* (15 species: 8 Coleoptera, 5 Lepidoptera and 2 Hymenoptera), followed by the Nearctic region (11 species: mainly Coleoptera) and the E Palearctic region (8 species: 3 Coleoptera, 3 Lepidoptera and 2 Hymenoptera). However, there is considerable overlap in the native regions of these species. For example, eight high-impact species native to W Palearctic are also native to E Palearctic. The Neotropic has two high-impact species, the bark beetle *Ips mexicanus* in the northern part of this region (in the native range of pines) and *Ormiscodes cinnamomea*, a polyphagous saturniid in Chile.

Establishments of species outside their native ranges

Establishments of non-native species (irrespective of impact)

Our compilation revealed almost one quarter (146 species) of insects feeding on *P. radiata* are established outside their native range, seven of which are considered cosmopolitan (Table 1). Beetles are the order with the most established non-native species with a total of 62 species including 20 bark and ambrosia beetles (Scolytinae), 15 other weevils (Curculionidae) and 14 longhorn beetles (Cerambycidae). This means that 22% of all beetles feeding on *P. radiata* are already established somewhere outside their native range (Table 1). With 36 established species, Hemiptera are also well represented among successful invaders. More than half (55%) of all the Hemiptera known from *P. radiata* are present outside their native range, significantly more than most other groups (Fig. 2A). Lepidoptera are another group of prominent invaders with 28 established species, but with a lower percentage of established species (12.5% of 224 Lepidoptera species known from *P. radiata*).

Borers were the dominant feeding guild among the established species, followed by sap-feeders and defoliators (Table 2). However, sap-feeders were the most successful invaders relative to the total number known in each feeding guild (i.e., 55% of all sap-feeders known to feed on *P. radiata* are already established somewhere. By contrast,

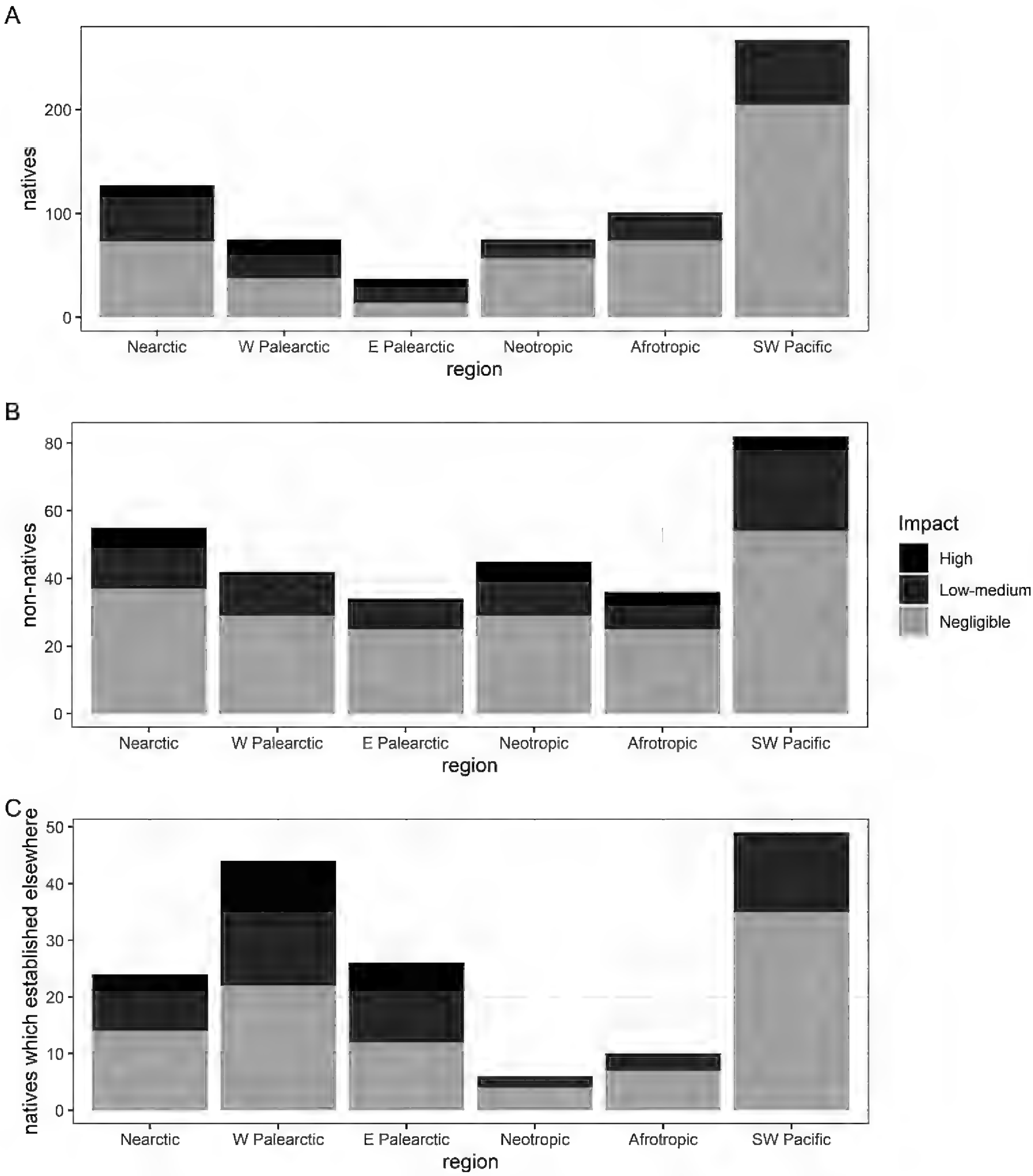

Figure 1. Impact levels of insect species feeding on *Pinus radiata* and their biogeographic ranges, excluding cosmopolitan species. (**A**) Species native to each biogeographic region. (**B**) Species non-native to each biogeographic region. (**C**) Species native to a biogeographic region (x-axis) which have established somewhere outside their native range (could be in the same biogeographic region e.g. from Australia to New Zealand). Note that the East Palearctic includes records from the Indo-Malayan region.

only 25% of known borers and 11% of known defoliators of *P. radiata* have successfully invaded somewhere (Table 2).

The SW Pacific region has the most known established non-native species (13% of all non-cosmopolitan species on the list), mainly due to a large number of species with negligible or low-medium impact (Fig. 1B). This is followed by the Nearctic (9%)

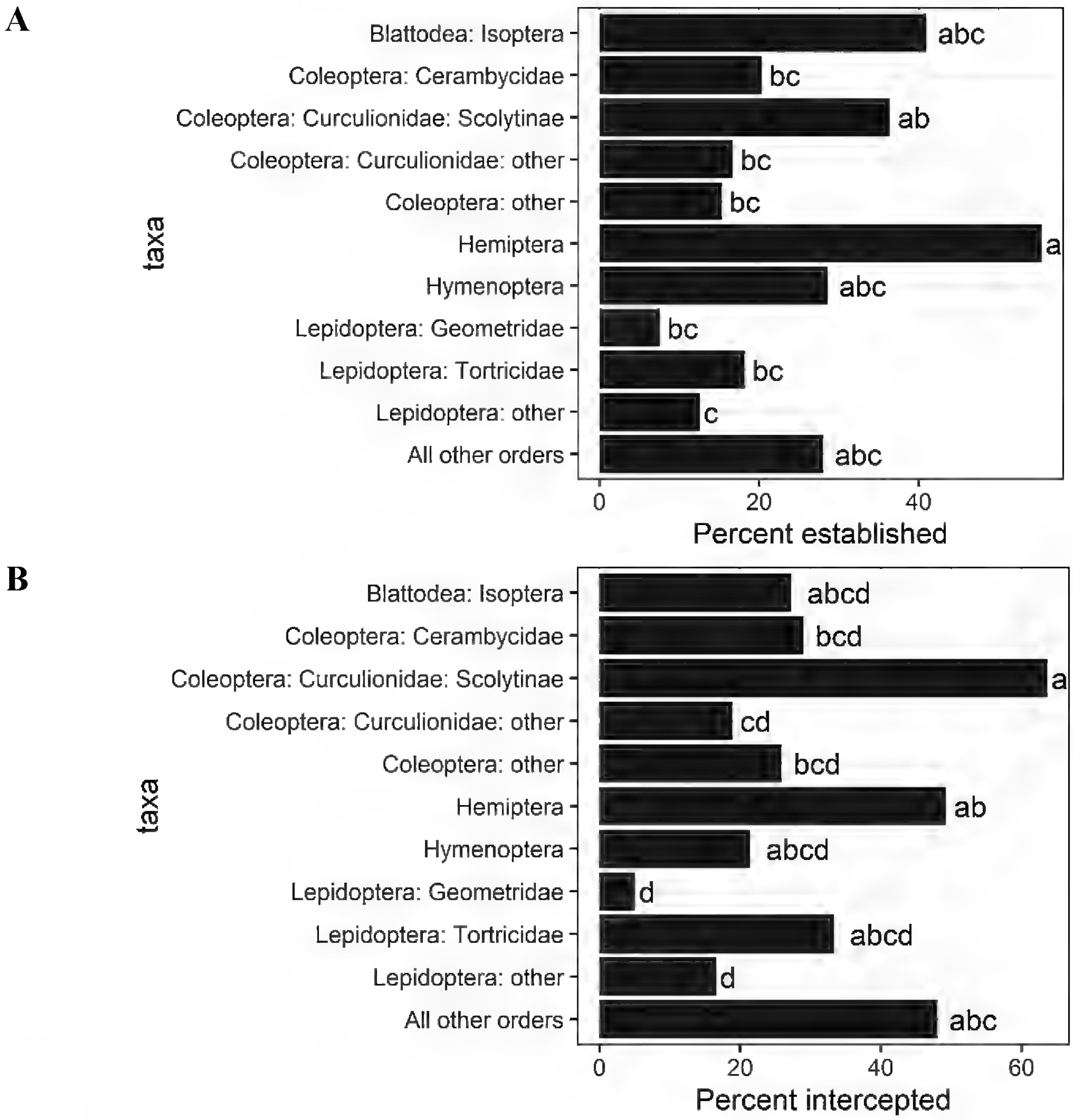

Figure 2. Percentages of each taxon established (**A**) or intercepted (**B**). Bars annotated with the same letter indicate proportions which were not significantly different (i.e. p>0.05) under multiple pairwise comparison of proportions using Fisher's Exact Tests with the Holm (1979) method of P-value adjustment.

and the Neotropic (7%) and West Palearctic regions (7%), whereby the former two have a large proportion of non-native high-impact species. Generally, the proportions of species with high- and low-medium-impact vary considerably among the regions. There was no significant difference in the proportions of species established among the non-negligible compared to among the negligible species (one-sided, 2-sample test for equality of proportions without continuity correction, Chi-squared = 2.622, P=0.053).

High-impact invaders

Twelve of the 28 high-impact species have already become established somewhere in the world, and six of these have become established in more than one biogeographic region (Table 3). The biogeographic regions with the most invasions of high-impact species (6) are the Nearctic or Neotropic (Fig. 1B); all but one of these species are

native to Europe (and adjacent parts of the W Palearctic region), with the remainder being a native species from the Nearctic which invaded the Neotropic. Other regions with several establishments of high-impact species are the SW Pacific (four species, two native to the W Palearctic and two native to the Nearctic), and the Afrotropic (four species with three of these being native to Europe), while the Western and the E Palearctic had only one established high-impact species each (Fig. 1B).

Native regions of established non-native species (including within the region)

The SW Pacific is the region with the most native species that became established somewhere outside their native range (both beyond and especially in other countries within their native biogeographic region), followed by the W Palearctic and the E Palearctic (Fig. 1C). However, the W Palearctic contributed by far the most high-impact species that became established somewhere, followed by the E Palearctic and the Nearctic. Although the E Palearctic ranks second in terms of high-impact species that established somewhere outside their native region, these are all species with a native range that extends from Europe across northern Asia, and it is difficult to ascertain the actual part of the region from which the invasion occurred.

Considering the source regions and invaded regions together, a clear picture of invasion routes emerges (Fig. 3). The W Palearctic is the main source region of invaders that colonised mainly the Nearctic, the Neotropic and the SW Pacific regions for all species (Fig. 3A) and species of non-negligible impact (Fig. 3B). Furthermore, the SW Pacific region has by far the most species that invaded other parts of the same region (Figs 3A, B, 4). However, these concern only species of negligible or low-medium impact as there are no high-impact species native to this region which established anywhere.

Border interceptions

Of all the species in the pine pest list, 185 (29%) were intercepted during border import inspections at least once internationally between 1995–2021 (Table 1). Of these, 83 species (13% of the pine pest list) were intercepted specifically at New Zealand's border between 2000–2017. An additional eight species were intercepted earlier (i.e., between 1950 and 2000 and recorded in New Zealand's BUGS database), and a further two species were intercepted and recorded in United States interception records from 1949–2008. Therefore, a total of 195 species were intercepted at least once at a border. More than 60% of species of Scolytinae (bark and ambrosia beetles) on the list were intercepted (at least once, Table 1), a significantly greater percentage than other beetle groups and several other taxa (Fig. 2B). In terms of feeding guilds, the percentage of intercepted species was greatest for sap-feeders and borers, and least for defoliators, while differences from 'other' guild members were not significant (Table 2). The most frequently intercepted species were mainly sap-feeders (including *Thrips tabaci*, Thysanoptera: Thripidae, 42,302 interceptions; *Aonidiella aurantii*, Hemiptera: Diaspididae, 8,782 interceptions; *Pseudococcus longispinus*, Hemiptera: Pseudococcidae, 3,341 interceptions; and sev-

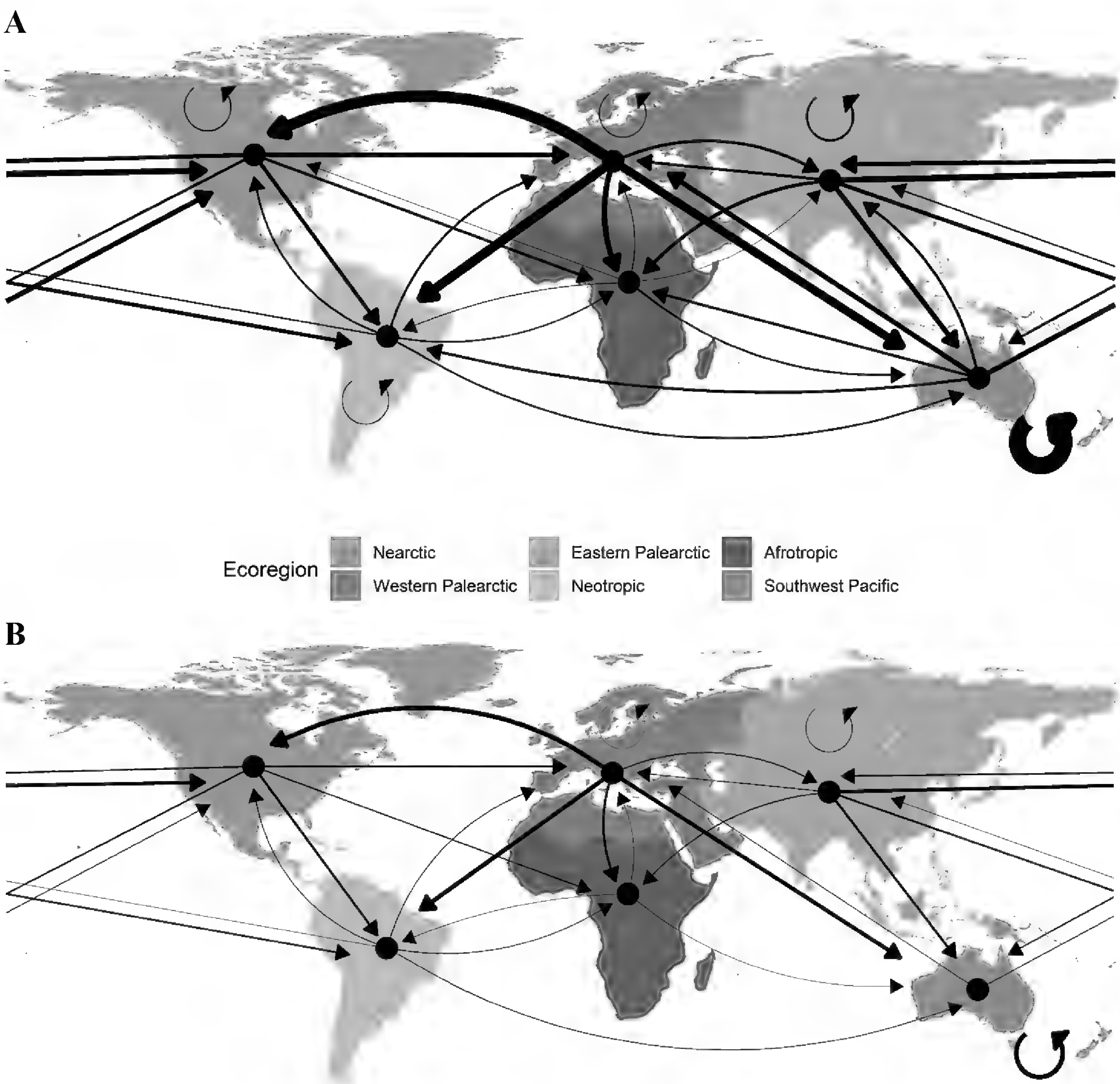

Figure 3. Global movement of all insects feeding on *Pinus radiata* (**A**), and those with non-negligible impact (**B**). The thickness of each arrow is relative to the number of species native to the source biogeographic region established in the destination biogeographic region. Some species had native ranges spanning multiple biogeographic ranges, and in general it is not known if regions were used as bridgeheads, so the arrows represent all possible movements. Note that the East Palearctic includes records from the Indo-Malayan region.

eral other Hemiptera), as well as the defoliators *Helicoverpa armigera* and *Helicoverpa punctigera* (Lepidoptera: Noctuidae, 8,668 and 1,793 interceptions, respectively) and a borer, the bark beetle *Hylurgus ligniperda* (Coleoptera: Curculionidae, 1,766 interceptions) (see Suppl. material 1: table S1 for a complete list of interceptions). The proportion of species that were intercepted was significantly higher among the non-negligible species than for negligible species (One sided, 2-sample test for equality of proportions without continuity correction on log-transformed data, Chi-squared = 8.210, p-value=0.002).

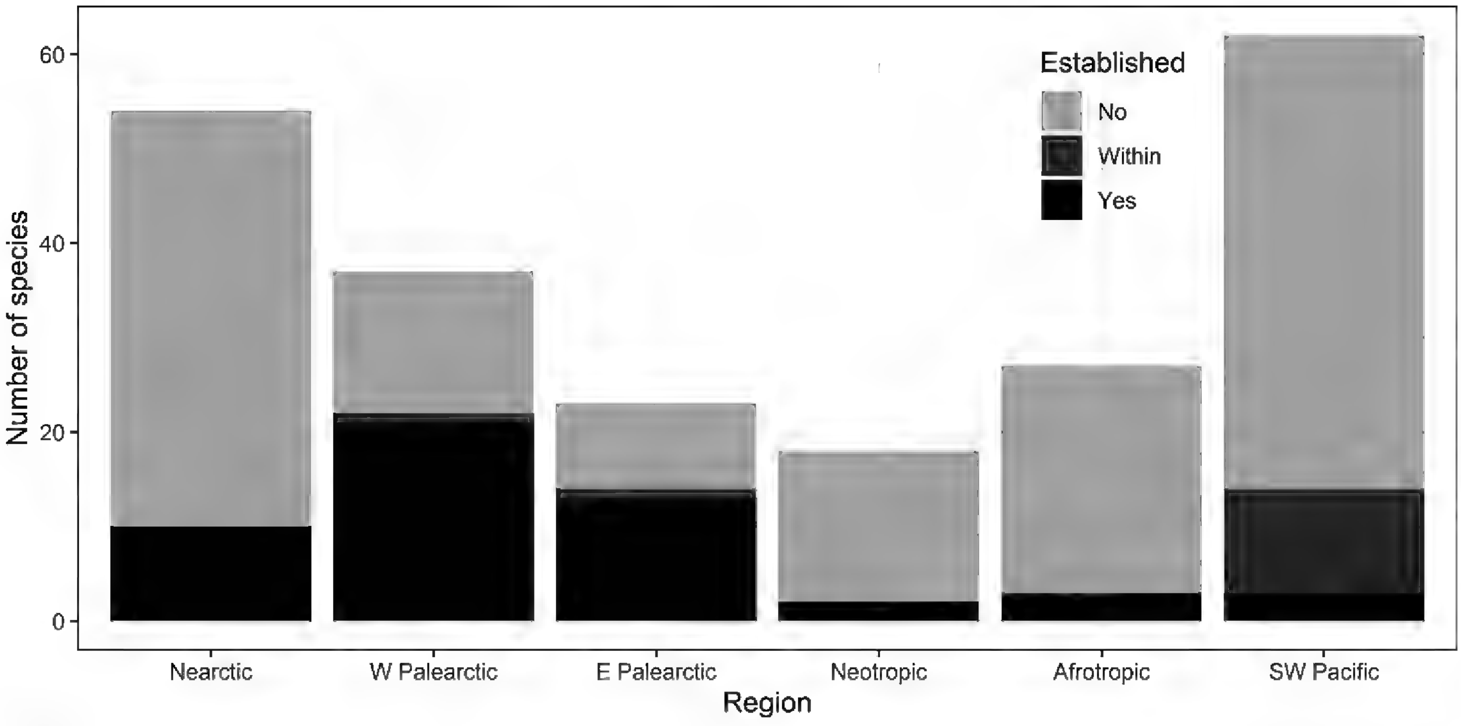

Figure 4. The number of species feeding on *Pinus radiata* that are native to each region and established (or not) outside their native range for non-negligible impact. Cosmopolitan species are excluded. Note, many of the native species from the SW Pacific are native to Australia but established in New Zealand – this is an example of a "Within" region establishment. Also note that some species are native to more than one biogeographic range, e.g., Palearctic species native to Europe and Asia, but this is not shown here. Note that the East Palearctic includes records from the Indo-Malayan region.

Relationships between interceptions and establishments

Among the species feeding on *P. radiata*, the number of intercepted species in a taxonomic group was strongly positively correlated with the number of established species in a family (Pearson's correlation coefficient, using log-transformed data: 0.92, $P<0.001$, Fig. 5). Of the 185 intercepted insect species (considering the international interception dataset from 1995–2021), 104 (56%) have already established somewhere (including cosmopolitan species), and 71% of the 146 species which have already invaded somewhere were intercepted (Fig. 6). Conversely, only 9% of the 464 species that were not intercepted have already invaded somewhere (Fig. 6). This indicates that species that are often intercepted also have a considerably higher likelihood of becoming established. Taxa with particularly high percentages of interceptions include the Scolytinae, Hemiptera and 'other' orders (mainly Orthoptera and Thysanoptera) (Table 1, Fig. 2B). Scolytinae and Hemiptera also have a high percentage of species that became established (Table 1, Fig. 2A).

Relationships between impacts, interceptions and establishments

Of the 28 high-impact species, 15 (54%) have been intercepted internationally (Table 3), and of the 168 species of low-medium impact, 56 (33%) have been intercepted (Suppl. material 1: table S1).

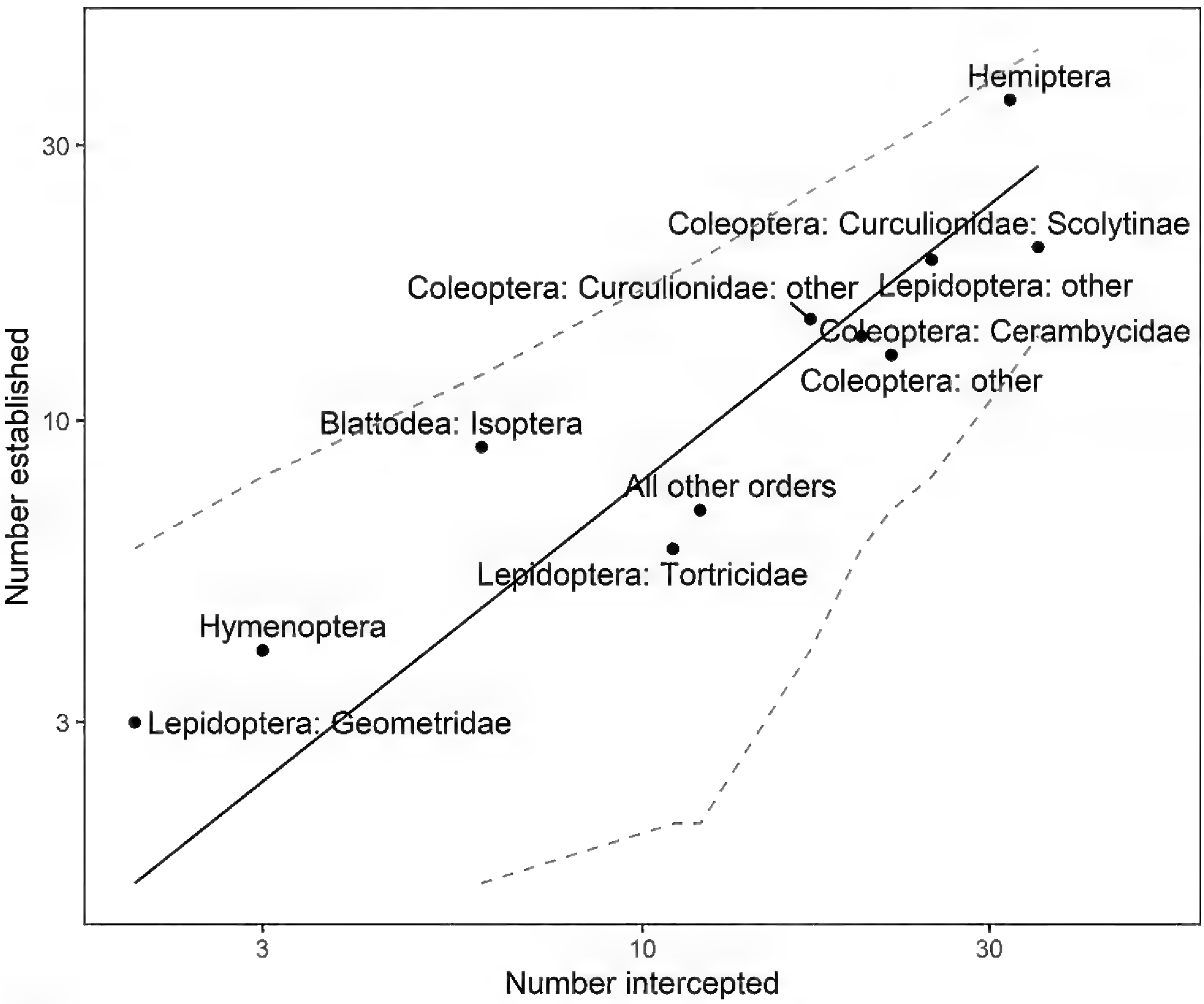

Figure 5. Number of species in the complete all-species pine pest list (649 species total) per taxonomic group that were intercepted and/or established, shown on a log-log scale. The black line represents where the taxa would fall on average if the number of established species was proportional to the number of intercepted species. The dashed lines show the prediction interval within which the taxa groups are expected to fall if establishments occurred at proportionally similar rates to interceptions, based on a Poisson model, alpha = 0.05, with Bonferroni correction accounting for 11 comparisons between taxa.

Of the 196 species with non-negligible impact, 19 species have been intercepted internationally more than 100 times (in decreasing order: *Thrips tabaci*, *Helicoverpa armigera*, *Helicoverpa punctigera*, *Hylurgus ligniperda*, *Hylastes ater*, *Arhopalus ferus*, *Lymantria dispar*, *Ips sexdentatus*, *Heliothrips haemorrhoidalis*, *Epiphyas postvittana*, *Gnathotrichus sulcatus*, *Dendroctonus valens*, *Bradysia impatiens*, *Gnathotrichus retusus*, *Agrotis infusa*, *Nysius vinitor*, *Orthotomicus erosus*, *Arhopalus rusticus* and *Leptoglossus occidentalis*) (Suppl. material 1: table S1). All but four of these 19 species have become established outside their native range (i.e., only *Ips sexdentatus*, *Gnathotrichus sulcatus*, *Gnathotrichus retusus* and *Nysius vinitor* have not yet invaded anywhere, to our knowledge).

A significantly greater percentage (36%) of species with non-negligible impact were intercepted than species with negligible impact (25%, P=0.002, see details above; Fig. 6), but the difference in impacts between species that had become established (or not) was marginally non-significant (P=0.053, see details above; Fig. 6, Suppl. mate-

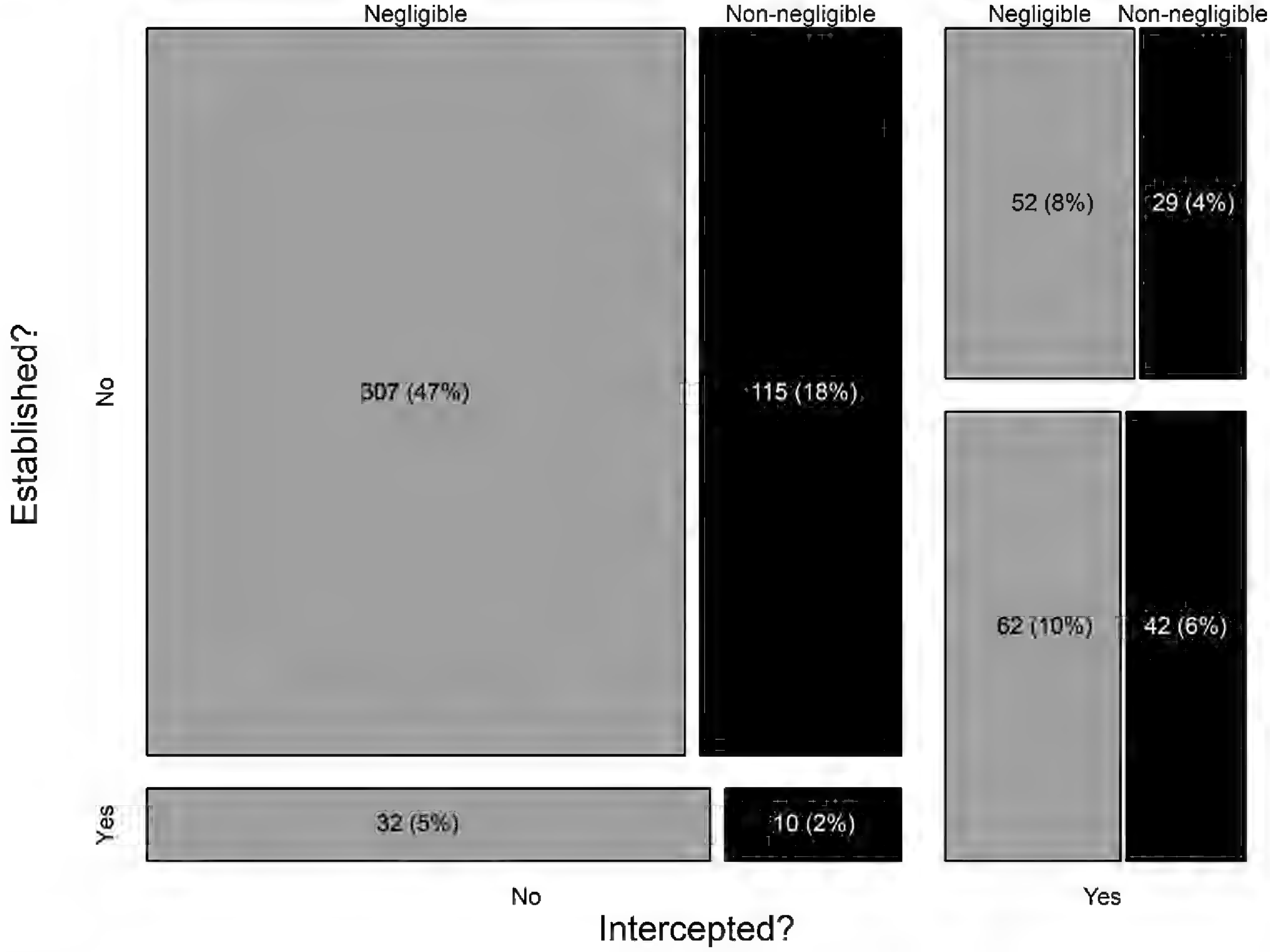

Figure 6. Mosaic plot of the number (and percentages) of species according to their intercepted, establishment, or impact status. Established species are those established in a region outside their native range and are inclusive of cosmopolitan species and species that were subsequently eradicated. Interceptions are based on the international interceptions dataset covering the period 1995–2021. Species with negligible impact on *Pinus radiata* in light grey, those with non-negligible impact (i.e., low-medium and high impact) in dark grey.

rial 3: table S3). For some taxa, differences were observed for both parameters. For example, among Cerambycidae with non-negligible impact, a higher percentage has been intercepted (78%) (compared with only 29% of all Cerambycidae feeding on *Pinus radiata*), and a higher percentage (44%) have established outside their native range (compared with 20% of all Cerambycidae). For Scolytinae feeding on *Pinus radiata*, nearly two thirds (64%) were intercepted, 51% were of non-negligible impact, and 36% are already established (Table 1), significantly higher proportions than for Cerambycidae (Chi-squared tests with Yates' continuity correction, impacts: Chi-squared = 19.19, df = 1, P<0.001; interceptions: Chi-squared = 13.52, df = 1, P< 0.001). This suggests that Scolytinae feeding on *Pinus radiata* are more likely to be intercepted, become established and have negative impacts than Cerambycidae. By contrast, only nine (22%) of the 40 Geometridae on the list have non-negligible impacts (and none fall into the high impact class), and few have been intercepted (5%) or become established (8%) (Table 1).

Results specific to New Zealand and Australia

High-impact species establishments and interceptions

No native high-impact species occur in New Zealand but one such species occurs and is native to Australia (the psychid moth *Hyalarcta huebneri*, Table 3, Suppl. material 1: table S1). Only three and four out of the 28 high-impact insect species are established in New Zealand and Australia, respectively (*Essigella californica*, *Hylastes ater* and *Sirex noctilio* in both, and *Ips grandicollis* in Australia only). Eight other high-impact species (*Hylastes angustatus*, *Lymantria dispar*, *Neodiprion sertifer*, *Orthotomicus erosus*, *Pissodes castaneus*, *Pissodes nemorensis*, *Rhyacionia buoliana* and *Tomicus piniperda*) are established elsewhere outside their native range (but not in New Zealand or Australia) (Suppl. material 1: table S1). Of these established species, all except *Essigella californica*, *Pissodes nemorensis* and *Rhyacionia buoliana* have been recorded in international interceptions (1995–2021) (Suppl. material 1: table S1). Of the internationally established species not yet in New Zealand, *Lymantria dispar* and *Orthotomicus erosus* were the two most frequently intercepted species in the international interceptions (1995–2021 data). In addition, *Ips grandicollis* was also frequently intercepted in New Zealand pre-2000, and is established in Australia and in parts of the E Palearctic. Likewise, *Tomicus piniperda* was also frequently intercepted in New Zealand pre-2000, and has already become established in the Nearctic region. *Ips sexdentatus*, while not yet established outside its native range, has been intercepted internationally (1995–2021) more than 100 times. In addition, ten highly-intercepted species with low-medium impact have already become established in New Zealand and/or Australia (nine and five species, respectively, Suppl. material 1: table S1).

Interceptions and establishment in New Zealand and Australia versus elsewhere

Forty (6%) of the insects on our pine pest list have invaded Australia, and 72 (11%) have invaded New Zealand. Seventy-one percent of the insect species intercepted in New Zealand (irrespective of impacts) have already invaded somewhere, and 58% have already invaded New Zealand. Of the insects intercepted internationally, 32% have invaded New Zealand already. Considering species which have already invaded somewhere, 40% were intercepted in New Zealand between 2000–2017. Of the insects which have already invaded New Zealand, 67% were intercepted in New Zealand between 2000–2017, and 82% were intercepted internationally between 1995–2021.

Feeding guild composition in New Zealand, Australia and elsewhere

The proportions of feeding guilds among native species feeding on *P. radiata* differed significantly between New Zealand and Australia and all other countries and regions (Suppl. material 4: fig. S1) (Pearson's Chi-squared test, Chi-squared = 10.40, df = 6, P = 0.015). In New Zealand, borers represent the largest proportion of native species

recorded from *P. radiata* (56%), whereas in Australia there is a high proportion of native defoliators (51%) (Suppl. material 4: fig. S1). In the remaining countries, borers and defoliators are about even.

Discussion

Species recorded on *Pinus radiata* in its native and introduced ranges

With a total of 649 insect species, our compilation of world-wide records of insects feeding on *Pinus radiata* represents a considerable increase over the last such comprehensive effort by Ohmart about 40 years ago (Ohmart 1980, 1981, 1982a, b). Although many of the most damaging insects of *P. radiata* were recognised then, several new threats have emerged. For example, the spongy moth *Lymantria dispar* was known as an occasional defoliator of *P. radiata* but it was considered "of little consequence" (Ohmart 1980). However, major outbreaks of *L. dispar* causing considerable defoliation have been reported recently from Spain (Castedo-Dorado et al. 2016) and we now classify this defoliator as a high-impact species. Another species that has only been recognised in this century as a potentially serious pest of *P. radiata* is the nun moth, *Lymantria monacha* (Withers and Keena 2001). Although other pine species have long been known to suffer sometimes severe defoliation by *L. monacha* in Europe, it was established through laboratory feeding trials that *P. radiata* is a highly suitable host for this defoliator (Withers and Keena 2001). Insects acting as vectors of the pitch canker disease, caused by the fungus *Fusarium circinatum*, are also of particular concern. The severe impacts of this disease on *P. radiata* have been known for some time (Wingfield et al. 2008b), and this is one of the main reasons why *P. radiata* is considered by the IUCN to be 'endangered' in its native range in California (Farjon 2013). However, the important role of insects such as the cone beetle *Conophthorus radiatae* as critical vectors in the transmission of the pathogen has only been appreciated in the last 25 years (Hoover et al. 1996; Brockerhoff et al. 2016). This is the main reason why insects capable of acting as vectors of *F. circinatum* are listed by us as high impact.

High-impact species and their native regions

Altogether, we rated 28 insect species as high impact. Most of these species are native to the Palearctic or Nearctic where pines are native, while only three species originate from parts of the southern hemisphere where *P. radiata* and other pines are planted as non-native species. This is consistent with observations on insects feeding on northern hemisphere plants in southern hemisphere regions such as New Zealand and Australia; these insects originate mainly from the northern hemisphere where their host plants or close relatives are native while comparatively few insects native to the southern hemisphere have colonised these plants which have few or no relatives in the native southern hemisphere flora (Brockerhoff et al. 2010; Harvey et al. 2012). Likewise, few

native insects in Europe damage non-native trees without close relatives (i.e., no congeneric species) in the European flora while those with close relatives are colonised by a larger suite of native plant-feeding insects (Branco et al. 2015; Padovani et al. 2020). This applies particularly to insects with a higher degree of host specificity but less so to polyphagous species.

More than half of the high-impact species are from the W Palearctic where they are normally found on European pine species. This means there are more high-impact species that have jumped from other pines to *P. radiata* (with which they have not co-evolved) than high-impact species with long associations with *P. radiata* in its native range. Such new associations between plant-feeding insects and new host plants often cause more severe damage than on their natural hosts. This is well illustrated by the pine processionary moth, *Thaumetopoea pityocampa*, which is considerably more damaging on *P. radiata* planted in Europe than on native European pines (Cobos-Suarez and Ruiz-Urrestarazu 1990), probably because *P. radiata* has not had the opportunity to evolve adaptations against this defoliator, in contrast to southern European pines which have co-evolved with *T. pityocampa*. The European six-toothed bark beetle *Ips sexdentatus* is mainly known as a secondary pest with relatively minor impacts (such as vectoring and facilitating blue-stain fungus infections) but during outbreaks in its native range, it can attack and kill live trees, albeit mainly those that are already weakened by other factors (Cobos-Suarez and Ruiz-Urrestarazu 1990). Other Palearctic species causing high impacts are more problematic in southern hemisphere regions where *P. radiata* has been planted than on *P. radiata* or other pines in Europe. Most notable among these are the Sirex woodwasp, *Sirex noctilio* (Slippers et al. 2015), and the European pine shoot moth, *Rhyacionia buoliana* (Alvarez and Ramirez 1989) which probably benefited from a combination of release from natural enemies (Mitchell and Power 2003; Colautti et al. 2004; Lombardero et al. 2008) and a highly susceptible tree species which has not co-evolved with these insects. High susceptibility in such cases may occur as novel host trees tend to have more limited resistance against non-native insects that are naturally associated with closely related trees, especially when the novel host has no experience with a congeneric native insect (Mech et al. 2019).

Even among the high-impact species native to the Nearctic, several are new associations where *P. radiata* represents a novel host. This includes, most notably, *Ips grandicollis*, the eastern five-spined engraver or five-spined bark beetle, which is native to eastern North America, with its range not sympatric with the natural distribution of *P. radiata*. *Ips grandicollis* invaded Australia where it can be highly damaging in *P. radiata* plantations and sometimes causes tree mortality by itself or in combination with attack by *Sirex noctilio* (Neumann 1987). Another species in this category is *Pissodes nemorensis*, an eastern North American weevil that can damage small trees and also acts as a vector of the pitch canker fungus, both of which have invaded South Africa (Gebeyehu and Wingfield 2003; Brockerhoff et al. 2016).

It is important to note that many of the high-impact species cause more substantial damage on *P. radiata* outside their native range. This applies, for example, to *Sirex noctilio*, *Ips grandicollis*, *Essigella californica* and *Rhyacionia buoliana*. These

species probably benefit from freedom of natural enemies compared with the situation in their native regions (Mitchell and Power 2003; Colautti et al. 2004). An equivalent situation may occur in regions where the insect is native but the tree is non-native and probably colonised less by natural enemies as in the case of *T. pityocampa* in *P. radiata* plantations in Europe. In addition, the simplified monoculture environment typical especially of southern hemisphere plantation forests probably has a lower abundance and diversity of natural enemies than more diverse forests which tend to be more common in the native region of *P. radiata* and other pines (Stemmelen et al. 2022).

Native regions of all species (irrespective of impact)

When considering all insects (not only those with high impact), the SW Pacific (i.e., in Australia or New Zealand) was the region with the greatest number of native species feeding on *P. radiata* (42% of all non-cosmopolitan species). This is rather surprising as there are no native pines or other Pinaceae in that region, and consequently, one would not expect a large number of species feeding on *P. radiata*. There are indeed a few native SW Pacific species that have caused noticeable damage in *P. radiata* plantations such as *Pseudocoremia suavis* (Lepidoptera: Geometridae) during outbreaks in New Zealand in the 1950s and 60s (White 1974). However, no outbreaks of this species have been recorded for nearly 50 years, and it is now relatively rare (Berndt et al. 2004), suggesting that these outbreaks were unusual occurrences. Consequently, we have rated *P. suavis* as low-medium impact. The majority of SW Pacific species (about 80%) have no or negligible impacts and the remainder are almost entirely in the low-medium impact category. The reason for the large number of records of species of little relevance is the existence of rigorous forest health surveillance systems in Australia and New Zealand where trees in plantation forests, urban areas, plant nurseries and high-risk sites near ports, airports and transitional facilities (where imports arrive and are cleared by biosecurity officials) are inspected regularly and any insects found are submitted for diagnostic identification (Bulman 2008; Carnegie and Nahrung 2019). These surveillance programmes are designed to detect incursions of non-native insect pests and pathogens as well as damage from known pests and pathogens but they also yield records of native species found on *P. radiata* even though most of these are not damaging. In other regions where *P. radiata* occurs as a native or non-native species, such non-damaging species are not recorded and published to the same extent and publications focus more on species causing more severe damage. Otherwise, the large number of species native to the Nearctic is consistent with this being the region where *P. radiata* and many other pines are native and as a result, there is a large fauna of insects feeding on pines. By contrast, the small number of species native to the E Palearctic may seem somewhat surprising given that there are many native pines and other Pinaceae in that region. However, *P. radiata* is not planted on a large scale in that region, and we are only aware of experimental plantings in China on an area covering hundreds of hectares (Bi et al. 2003, 2008). As the number of species colonising non-native trees is positively corre-

lated with the area planted (Branco et al. 2015), it is plausible that there are comparatively few records of insects feeding on *P. radiata* from China and the E Palearctic (Bi et al. 2008). In addition, our list is probably not entirely complete because sources in languages other than English, especially in the grey literature, may have been missed. This potential bias may have affected especially our records from the E Palearctic and Neotropic with a higher proportion of non-English literature. Furthermore, some regions are under-studied regarding biological invasions, especially in the E Palearctic and Afrotropic regions (Pyšek et al. 2008).

Non-native invasive insects on *P. radiata*

With 146 established non-native insects feeding on *P. radiata*, 22% of all species in our database have already successfully invaded other regions. This large number of invasions is likely to be related to the substantial international trade in pine logs, timber, wood packaging material and propagation material used for the establishment of *P. radiata* plantations in non-native regions. International trade in logs, timber and goods shipped with wood packaging materials such as pallets are important pathways facilitating invasions especially of bark beetles, longhorn beetles and other wood borers (Brockerhoff et al. 2006, 2014; Meurisse et al. 2019; Vilardo et al. 2022), the groups most represented among established non-native species. Trade in live plants used for propagation is another important invasion pathway which is particularly relevant for sap-feeders in the order Hemiptera and defoliating and other Lepidoptera (Liebhold et al. 2012; Meurisse et al. 2019), the second- and third most numerous groups of non-native species feeding on *P. radiata*.

Nearly half of the 28 high-impact species we identified already occur somewhere as established non-native species. However, only six are established in more than one non-native region, indicating a large potential for additional invasions. Also, there are differences between regions in the number of established species. For example, there are only four established high-impact species in the SW Pacific while the remaining 86% are not yet present, which suggests there is considerable benefit in continuing and enhancing biosecurity measures aimed at preventing the arrival and establishment of these species (Sequeira and Griffin 2014; Ormsby and Brenton-Rule 2017).

Border interceptions with imported goods

Nearly a third of the species on our list (29%) were intercepted at least once in the countries for which we could access border interception data. For bark beetles, the percentage of intercepted species was even higher and exceeded 60%. Fifteen of the 28 high-impact species were intercepted, in some cases hundreds of times (e.g., *Ips sexdentatus*, *Lymantria dispar* and *Hylastes ater*). This highlights that pathways exist by which many of these species are transported with international trade and that there is a high potential for additional invasions to occur. Positive relationships between the number of interceptions of species and the probability of invasions have been documented, especially for groups such as bark beetles and longhorn beetles which are often well-

identified and are less affected by insufficient identification or omission in interception data (e.g., Brockerhoff et al. 2014; Turner et al. 2020; Nahrung and Carnegie 2021). Our analyses specific to insects feeding on *P. radiata* were consistent with these trends as we found a positive correlation between the number of intercepted species within a taxonomic group and established species in that group (Nahrung and Carnegie 2021). Although some key pathways, such as the use of wood packaging materials, have been mitigated with some effect (Haack et al. 2014), the sheer volume of international trade means that some risk of introduction remains.

Conclusions and outlook

Our compilation and analyses of insects feeding on *P. radiata* has identified numerous species that pose a threat to this tree species in many world regions. Although a large number of damaging native and non-native species have already become associated with *P. radiata* where it is native or has been planted as an introduced tree species, a larger proportion of damaging species could still invade regions where they do not yet occur. Border interceptions of many of these species indicate that pathways exist by which these species move via international trade. Furthermore, there is no sign of saturation of invasions occurring, and additional species continue to be detected as new invaders at a high frequency (Seebens et al. 2018) due to the increasing globalisation of international trade which leads to the expansion of source pools from which potential invaders are being transported. This is partly also noticeable in our analysis where, historically, the W Palearctic has been the dominant source of insects feeding on *Pinus radiata* (particularly of those with non-negligible impact), but this is likely to change with changing global trade relationships.

Although the depth of our global analyses and the large number of species we assessed provide some confidence in our findings and interpretations, there is still considerable uncertainty about the identity of future invaders and damaging species. This stems from the ongoing difficulty of predicting impacts of species that have not yet become established outside their native range. This is illustrated by the cases of species such as *Sirex noctilio*, *Ips grandicollis* and *Essigella californica*, which, based on the low level of damage caused in their native range, would not have been predicted to be so damaging as invaders. Likewise, many insects feeding on other species of pine or Pinaceae probably have the potential to cause damage on *P. radiata* but have not yet crossed paths. For example, in northeast Asia, native species of *Pinus* and other Pinaceae are very common, but there are only few plantings of *P. radiata* and limited research so far on insects feeding on this tree (Bi et al. 2008). It would be very useful to be able to better predict which traits and characteristics predispose such insects to cause substantial damage to *P. radiata*.

New Zealand, Australia and Chile are at a particular risk from such species because of their major reliance on *P. radiata* as a commercial forestry species. Examples of frequently intercepted species that pose a high risk to these and other southern hemisphere countries where *P. radiata* is grown include *Dendroctonus valens* (which

has already become established in the E Palearctic), *Hylurgops palliatus* (established in the Nearctic), *Leptoglossus occidentalis* (established in the Afrotropic, W Palearctic, E Palearctic and Neotropic) and *Ips grandicollis* (established in Australia). Although *D. valens* and *L. occidentalis* are only considered low-medium impact on *Pinus radiata*, they are considered highly damaging and have high impact on other *Pinus* species. Furthermore, high-impact species that would probably be highly damaging, but have not yet been intercepted, include *Lymantria monacha*, *Rhyacionia buoliana* and *Thaumetopoea pityocampa*. Finally, there are likely to be many species of 'unknown' risk to *P. radiata* which have not yet come into contact with it yet.

Acknowledgements

The authors are grateful to the late John Bain for his substantial compilation of insects on *Pinus radiata* in New Zealand and internationally which he curated for more than two decades. We would also like to thank Milla Baker for literature searches and curation of the list; Richard Mally, Robert Hoare and Jan Krecek for taxonomic advice; and two anonymous reviewers. This research was funded in part by the New Zealand Ministry of Business Innovation and Employment Strategic Science Investment Funding (CO4X1703, Forest Systems Platform) to Scion and by the HOMED project (http://homed-project.eu/) which received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No. 771271.

References

Allen JD (1973) Pests and diseases of Radiata pine. New Zealand Journal of Forestry 18: 265–272.

Alvarez G, Ramirez O (1989) Assessment of damage caused by European pine shoot moth in radiata pine plantations in Chile. In: Alfaro RI, Glover SG (Eds) Proceedings of meeting of IUFRO work group 'Insects affecting reforestation biology and damage', July 3–9, 1988. Forestry Canada, Pacific Forestry Center, Victoria, Canada, 145–154.

Bain J, Sopow SL, Bulman LS (2012) The sirex woodwasp in New Zealand: history and current status. In: Slippers B, De Groot P, Wingfield MJ (Eds) The Sirex Woodwasp and its Fungal Symbiont: Research and Management of a Worldwide Invasive Pest. Springer, Dordrecht, 167–173. https://doi.org/10.1007/978-94-007-1960-6_13

Berndt L, Brockerhoff EG, Jactel H, Weiss T, Beaton J (2004) Biology and rearing of *Pseudocoremia suavis*, an endemic looper (Lepidoptera: Geometridae) with a history of outbreaks on exotic conifers. New Zealand Entomologist 27(1): 73–82. https://doi.org/10.1080/00779962.2004.9722127

Bi H, Simpson J, Sullivan S, Li RW, Yan H, Wu Z, Cai S, Eldridge R (2003) Introduction of *Pinus radiata* for afforestation: A review with reference to Aba, China. Journal of Forestry Research 14(4): 311–322. https://doi.org/10.1007/BF02857861

Bi H, Simpson J, Eldridge R, Sullivan S, Li RW, Xiao YG, Zhou J, Wu Z, Yan H, Huang Q, Liu Q (2008) Survey of damaging pests and preliminary assessment of forest health risks to

the long term success of *Pinus radiata* introduction in Sichuan, southwest China. Journal of Forestry Research 19(2): 85–100. https://doi.org/10.1007/s11676-008-0016-5

Bi H, Li R, Wu Z, Huang Q, Liu Q, Zhou Y, Li Y (2013) Early performance of *Pinus radiata* provenances in the earthquake-ravaged dry river valley area of Sichuan, southwest China. Journal of Forestry Research 24(4): 619–632. https://doi.org/10.1007/s11676-013-0400-7

Bouchard P, Bousquet Y, Davies AE, Alonso-Zarazaga MA, Lawrence JF, Lyal CH, Newton A, Reid C, Schmitt M, Slipinski A, Smith A (2011) Family-group names in Coleoptera (Insecta). ZooKeys 88: 1–972. https://doi.org/10.3897/zookeys.88.807

Branco M, Brockerhoff EG, Castagneyrol B, Orazio C, Jactel H (2015) Host range expansion of native insects to exotic trees increases with area of introduction and the presence of congeneric native trees. Journal of Applied Ecology 52(1): 69–77. https://doi.org/10.1111/1365-2664.12362

Brockerhoff EG, Bulman L (2014) Biosecurity risks to New Zealand's plantation forests and the rationale for pathway risk management. New Zealand Journal of Forestry 59(2): 3–8.

Brockerhoff EG, Liebhold AM (2017) Ecology of forest insect invasions. Biological Invasions 19(11): 3141–3159. https://doi.org/10.1007/s10530-017-1514-1

Brockerhoff EG, Bain J, Kimberley M, Knížek M (2006) Interception frequency of exotic bark and ambrosia beetles (Coleoptera: Scolytinae) and relationship with establishment in New Zealand and worldwide. Canadian Journal of Forest Research 36(2): 289–298. https://doi.org/10.1139/x05-250

Brockerhoff EG, Barratt BI, Beggs JR, Fagan LL, Malcolm K, Phillips CB, Vink CJ (2010) Impacts of exotic invertebrates on New Zealand's indigenous species and ecosystems. New Zealand Journal of Ecology 34(1): 158–174.

Brockerhoff EG, Kimberley M, Liebhold AM, Haack RA, Cavey JF (2014) Predicting how altering propagule pressure changes establishment rates of biological invaders across species pools. Ecology 95(3): 594–601. https://doi.org/10.1890/13-0465.1

Brockerhoff EG, Dick M, Ganley R, Roques A, Storer AJ (2016) Role of insect vectors in epidemiology and invasion risk of *Fusarium circinatum*, and risk assessment of biological control of invasive *Pinus contorta*. Biological Invasions 18(4): 1177–1190. https://doi.org/10.1007/s10530-016-1059-8

Brockerhoff EG, Gresham BA, Meurisse N, Nahrung HF, Perret-Gentil A, Pugh AR, Sopow S, Turner RM (2023) *Pinus radiata* pest list [Data set]. Zenodo. https://doi.org/10.5281/zenodo.7545927

Bulman LS (2008) Pest detection surveys on high-risk sites in New Zealand. Australian Forestry 71(3): 242–244. https://doi.org/10.1080/00049158.2008.10675042

CABI (2019) *Pinus radiata* (radiata pine). CABI Compendium. https://doi.org/10.1079/cabicompendium.41699 [Accessed 13/01/2023]

Carnegie AJ, Nahrung HF (2019) Post-border forest biosecurity in Australia: Response to recent exotic detections, current surveillance and ongoing needs. Forests 10(4): e336. https://doi.org/10.3390/f10040336

Carter PC, Griffith JA (1989) Risk assessment and pest detection surveys for exotic pests and diseases which threaten commercial forestry in New Zealand. New Zealand Journal of Forestry Science 19(2/3): 353–374.

Castedo-Dorado F, Lago-Parra G, Lombardero MJ, Liebhold AM, Álvarez-Taboada MF (2016) European gypsy moth (*Lymantria dispar dispar* L.) completes development and defoliates exotic radiata pine plantations in Spain. New Zealand Journal of Forestry Science 46(1): 1–18. https://doi.org/10.1186/s40490-016-0074-y

Chamberlain SA, Szöcs E (2013) Taxize: Taxonomic search and retrieval in R. F1000 Research 2013(2): e191. https://doi.org/10.12688/f1000research.2-191.v1

Cobos-Suarez JM, Ruiz-Urrestarazu MM (1990) Problemas fítosanitarios de la especie *Pinus radiata* D. Don en España, con especial referencia al País Vasco. Boletin de Sanidad Vegetal, Plagas 16: 37–53. [Phytosanitary problems of the species *Pinus radiata* in Spain, with special reference to the Basque country]

Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? Ecology Letters 7(8): 721–733. https://doi.org/10.1111/j.1461-0248.2004.00616.x

CONAF (2021) Plantaciones forestales. CONAF, Chile. https://www.conaf.cl/nuestros-bosques/plantaciones-forestales [Accessed 5/12/2021]

Eyles A, Robinson AP, Smith D, Carnegie A, Smith I, Stone C, Mohammed C (2011) Quantifying stem growth loss at the tree-level in a Pinus radiata plantation to repeated attack by the aphid, Essigella californica. Forest Ecology and Management 261(1): 120–127. https://doi.org/10.1016/j.foreco.2010.09.039

Farjon A (2013) *Pinus radiata*. The IUCN Red List of Threatened Species 2013: e.T42408A2977955. https://doi.org/10.2305/IUCN.UK.2013-1.RLTS.T42408A2977955.en [Accessed 21/09/2022]

Forestry Economics Services CC (2020) Republic of South Africa Department of Forestry, Fisheries and the Environment, Forestry & Natural Resources Management Branch. Report on Commercial Timber Resources and Primary Roundwood Processing in South Africa 2018/2019. Compiled on behalf of the Directorate: Forestry Regulations and Oversight by Forestry Economics Services CC. Pretoria, South Africa, 115 pp.

Fox J, Weisberg S (2011) An R Companion to Applied Regression. Sage Publ., Thousand Oaks.

Gebeyehu S, Wingfield MJ (2003) Pine weevil *Pissodes nemorensis*: Threat to South African pine plantations and options for control. South African Journal of Science 99(11–12): 531–536.

Gordon TR, Storer AJ, Wood DL (2001) The pitch canker epidemic in California. Plant Disease 85(11): 1128–1139. https://doi.org/10.1094/PDIS.2001.85.11.1128

Haack RA, Britton KO, Brockerhoff EG, Cavey JF, Garrett LJ, Kimberley M, Lowenstein F, Nuding A, Olson LJ, Turner J, Vasilaky KN (2014) Effectiveness of the International Phytosanitary Standard ISPM No. 15 on reducing wood borer infestation rates in wood packaging material entering the United States. PLoS ONE 9(5): e96611. https://doi.org/10.1371/journal.pone.0096611

Harvey KJ, Nipperess DA, Britton DR, Hughes L (2012) Australian family ties: Does a lack of relatives help invasive plants escape natural enemies? Biological Invasions 14(11): 2423–2434. https://doi.org/10.1007/s10530-012-0239-4

Holm S (1979) A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics 6: 65–70. http://www.jstor.org/stable/4615733

Hoover K, Wood DL, Storer AJ, Fox JW, Bros WE (1996) Transmission of the pitch canker fungus, *Fusarium subglutinans* f. sp. *pini*, to Monterey pine, *Pinus radiata*, by cone- and twig-infesting beetles. Canadian Entomologist 128(6): 981–994. https://doi.org/10.4039/Ent128981-6

Hurley BP, Garnas J, Wingfield MJ, Branco M, Richardson DM, Slippers B (2016) Increasing numbers and intercontinental spread of invasive insects on eucalypts. Biological Invasions 18(4): 921–933. https://doi.org/10.1007/s10530-016-1081-x

IUCN (2020) IUCN EICAT Categories and Criteria. The Environmental Impact Classification for Alien Taxa First edition. IUCN, Gland, Switzerland and Cambridge, UK.

Kirisits T (2004) Fungal associates of European bark beetles with special emphasis on ophiostomatoid fungi. In: Lieutier F, Day KR, Battisti A, Gregoire J-C, Evans HF (Eds) Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis. Springer, Dordrecht, 181–236. https://doi.org/10.1007/978-1-4020-2241-8_10

Lavery PB, Mead DJ (1998) *Pinus radiata*–a narrow endemic of North America takes on the world. In: Richardson DM (Ed.) Ecology and Biogeography of *Pinus*. Cambridge University Press, UK, 432–449.

Lawson SA, Carnegie AJ, Cameron N, Wardlaw T, Venn TJ (2018) Risk of exotic pests to the Australian forest industry. Australian Forestry 81(1): 3–13. https://doi.org/10.1080/00049158.2018.1433119

Legg P, Frakes I, Gavran M (2021) Australian plantation statistics and log availability report 2021. ABARES research report. Australian Bureau of Agricultural and Resource Economics and Sciences (ABARES), Canberra, Australia.

Liebhold AM, Brockerhoff EG, Garrett LJ, Parke JL, Britton KO (2012) Live plant imports: The major pathway for forest insect and pathogen invasions of the US. Frontiers in Ecology and the Environment 10(3): 135–143. https://doi.org/10.1890/110198

Lombardero MJ, Vázquez-Mejuto P, Ayres MP (2008) Role of plant enemies in the forestry of indigenous vs. nonindigenous pines. Ecological Applications 18(5): 1171–1181. https://doi.org/10.1890/07-1048.1

Mally R, Turner R, Blake RE, Fenn-Moltu G, Bertelsmeier C, Brockerhoff EG, Hoare R, Nahrung HF, Roques A, Pureswaran DS, Yamanaka T, Liebhold AM (2022) Moths and butterflies on alien shores: Global biogeography of non-native Lepidoptera. Journal of Biogeography 49(8): 1455–1468. https://doi.org/10.1111/jbi.14393

Mead DJ (2013) Sustainable management of *Pinus radiata* plantations. FAO Forestry Paper No. 170. FAO, Rome.

Mech AM, Thomas KA, Marsico TD, Herms DA, Allen CR, Ayres MP, Gandhi KJK, Gurevitch J, Havill NP, Hufbauer RA, Liebhold AM, Raffa KF, Schulz AN, Uden DR, Tobin PC (2019) Evolutionary history predicts high-impact invasions by herbivorous insects. Ecology and Evolution 9(21): 12216–12230. https://doi.org/10.1002/ece3.5709

Meurisse N, Rassati D, Hurley BP, Brockerhoff EG, Haack RA (2019) Common pathways by which non-native forest insects move internationally and domestically. Journal of Pest Science 92(1): 13–27. https://doi.org/10.1007/s10340-018-0990-0

Mitchell CE, Power AG (2003) Release of invasive plants from fungal and viral pathogens. Nature 421(6923): 625–627. https://doi.org/10.1038/nature01317

Nahrung HF, Carnegie AJ (2020) Non-native forest insects and pathogens in Australia: Establishment, spread, and impact. Frontiers in Forests and Global Change 3: 1–37. https://doi.org/10.3389/ffgc.2020.00037

Nahrung HF, Carnegie AJ (2021) Border interceptions of forest insects established in Australia: Intercepted invaders travel early and often. NeoBiota 64: 69–86. https://doi.org/10.3897/neobiota.64.60424

Neumann FG (1987) Introduced bark beetles on exotic trees in Australia with special reference to infestations of *Ips grandicollis* in pine plantations. Australian Forestry 50(3): 166–178. https://doi.org/10.1080/00049158.1987.10674513

NZFOA (2021) Facts & Figures 2020/21. New Zealand plantation forest industry. Forest Owners Association, Wellington. https://www.nzfoa.org.nz/images/FGT_3704_Facts_and_Figures_202021_Web_FA1.pdf [Accessed 05/12/2021]

Ohmart CP (1980) Insect pests of Pinus radiata plantations: Present and possible future problems. Australian Forestry 43(4): 226–232. https://doi.org/10.1080/00049158.1980.10674276

Ohmart CP (1981) An annotated list of insects associated with *Pinus radiata* D. Don in California. Divisional Report no. 8. CSIRO Division of Forest Research, Commonwealth Scientific and Industrial Research Organisation, Canberra.

Ohmart CP (1982a) Destructive insects of native and planted *Pinus radiata* in California, and their relevance to Australian forestry. Australian Forest Research 12(2): 151–161.

Ohmart CP (1982b) Insects associated with Pinus radiata throughout the world: an annotated bibliography. Divisional Report no. 9. CSIRO Division of Forest Research, Commonwealth Scientific and Industrial Research Organisation, Canberra.

Ormsby M, Brenton-Rule E (2017) A review of global instruments to combat invasive alien species in forestry. Biological Invasions 19(11): 3355–3364. https://doi.org/10.1007/s10530-017-1426-0

Padovani RJ, Salisbury A, Bostock H, Roy DB, Thomas CD (2020) Introduced plants as novel Anthropocene habitats for insects. Global Change Biology 26(2): 971–988. https://doi.org/10.1111/gcb.14915

Pyšek P, Richardson DM, Pergl J, Jarošík V, Sixtová Z, Weber E (2008) Geographical and taxonomic biases in invasion ecology. Trends in Ecology & Evolution 23(5): 237–244. https://doi.org/10.1016/j.tree.2008.02.002

Saccaggi DL, Arendse M, Wilson JR, Terblanche JS (2021) Contaminant organisms recorded on plant product imports to South Africa 1994–2019. Scientific Data 8(1): 1–11. https://doi.org/10.1038/s41597-021-00869-z

Secretariat GBIF (2021) GBIF Backbone Taxonomy. https://doi.org/10.15468/39omei [Accessed 02/09/2022 via GBIF.org]

Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, van Kleunen M, Winter M, Ansong M, Arianoutsou M, Bacher S, Blasius B, Brockerhoff EG, Brundu G, Capinha C, Causton CE, Celesti-Grapow L, Dawson W, Dullinger S, Economo EP, Fuentes N, Guénard B, Jäger H, Kartesz J, Kenis M, Kühn I, Lenzner B, Liebhold AM, Mosena A, Moser D, Nentwig W, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, Walker K, Ward DF, Yamanaka T, Essl F (2018) Global rise in emerging alien species results from increased accessibility of new source pools.

Proceedings of the National Academy of Sciences of the United States of America 115(10): E2264–E2273. https://doi.org/10.1073/pnas.1719429115

Sequeira R, Griffin R (2014) The biosecurity continuum and trade: Pre-border operations. The Handbook of Plant Biosecurity. Springer, The Netherlands, 119–148. https://doi.org/10.1007/978-94-007-7365-3_5

Slippers B, Hurley BP, Wingfield MJ (2015) Sirex woodwasp: A model for evolving management paradigms of invasive forest pests. Annual Review of Entomology 60(1): 601–619. https://doi.org/10.1146/annurev-ento-010814-021118

Stemmelen A, Jactel H, Brockerhoff E, Castagneyrol B (2022) Meta-analysis of tree diversity effects on the abundance, diversity and activity of herbivores' enemies. Basic and Applied Ecology 58: 130–138. https://doi.org/10.1016/j.baae.2021.12.003

Turner RM, Plank MJ, Brockerhoff EG, Pawson S, Liebhold A, James A (2020) Considering unseen arrivals in predictions of establishment risk based on border biosecurity interceptions. Ecological Applications 30(8): e02194. https://doi.org/10.1002/eap.2194

Turner RM, Brockerhoff EG, Bertelsmeier C, Blake RE, Caton B, James A, MacLeod A, Nahrung HF, Pawson SM, Plank MJ, Pureswaran DS, Seebens H, Yamanaka T, Liebhold AM (2021a) Worldwide border interceptions provide a window into human-mediated global insect movement. Ecological Applications 31(7): e02412. https://doi.org/10.1002/eap.2412

Turner RM, Blake RE, Liebhold AM (2021b) International non-native insect establishment data (0.1) [data set]. Zenodo. https://doi.org/10.5281/zenodo.5245302

Udvardy MDF (1975) A classification of the biogeographical provinces of the world. IUCN Occasional Paper. International Union for Conservation of Nature and Natural Resources (IUCN), Morges.

Vilardo G, Faccoli M, Corley JC, Lantschner M (2022) Factors driving historic intercontinental invasions of European pine bark beetles. Biological Invasions 24(9): 2973–2991. https://doi.org/10.1007/s10530-022-02818-2

Watson MC, Kriticos DJ, Drayton GM, Teulon DAJ, Brockerhoff EG (2008) Assessing the effect of Essigella californica on *Pinus radiata* at two sites in New Zealand. New Zealand Plant Protection 61: 179–184. https://doi.org/10.30843/nzpp.2008.61.6833

White TCR (1974) A hypothesis to explain outbreaks of looper caterpillars, with special reference to populations of *Selidosema suavis* in a plantation of *Pinus radiata* in New Zealand. Oecologia 16(4): 279–301. https://doi.org/10.1007/BF00344738

Wingfield MJ, Hurley BP, Gebeyehu S, Slippers B, Ahumada R, Wingfield BD (2008a) Southern Hemisphere exotic pine plantations threatened by insect pests and their associated fungal pathogens. In: Paine TD (Ed.) Invasive Forest Insects, Introduced Forest Trees, and Altered Ecosystems. Springer, Dordrecht, 53–61. https://doi.org/10.1007/1-4020-5162-X_3

Wingfield MJ, Hammerbacher A, Ganley RJ, Steenkamp ET, Gordon TR, Wingfield BD, Coutinho TA (2008b) Pitch canker caused by *Fusarium circinatum*–A growing threat to pine plantations and forests worldwide. Australasian Plant Pathology 37(4): 319–334. https://doi.org/10.1071/AP08036

Withers TM, Keena MA (2001) *Lymantria monacha* (nun moth) and *L. dispar* (gypsy moth) survival and development on improved *Pinus radiata*. New Zealand Journal of Forestry Science 3(1): 66–77.

Supplementary material 1

Pest list of insects feeding on *Pinus radiata* worldwide

Authors: Eckehard G. Brockerhoff, Belinda A. Gresham, Nicolas Meurisse, Helen F. Nahrung, Anouchka Perret-Gentil, Andrew R. Pugh, Stephanie L. Sopow, Rebecca M. Turner

Data type: Occurrences and characteristics of species

Explanation note: Supplementary table providing a detailed list of insects feeding on *Pinus radiata* worldwide, their native range, introduced range (where applicable), impacts, interceptions, and references.

Link: https://doi.org/10.3897/neobiota.84.95864.suppl1

Supplementary material 2

Statistics for Table 2. Statistical tests of proportions out of all species among feeding types for impacts, establishments and interceptions.

Authors: Eckehard G. Brockerhoff, Belinda A. Gresham, Nicolas Meurisse, Helen F. Nahrung, Anouchka Perret-Gentil, Andrew R. Pugh, Stephanie L. Sopow, Rebecca M. Turner

Data type: Statistics

Explanation note: Details on statistical tests of proportions out of all species among feeding types for impacts, establishments and interceptions.

Link: https://doi.org/10.3897/neobiota.84.95864.suppl2

Supplementary material 3

Numbers (and percentages) of species by impact class, and whether or not they have been intercepted (based on the international interceptions dataset covering the period 1995–2021) or established in a region outside their native range.

Authors: Eckehard G. Brockerhoff, Belinda A. Gresham, Nicolas Meurisse, Helen F. Nahrung, Anouchka Perret-Gentil, Andrew R. Pugh, Stephanie L. Sopow, Rebecca M. Turner

Data type: Numbers and percentages of species by impact class

Explanation note: supplementary table providing numbers and percentages of species by impact class, and whether or not they have been intercepted or established in a region outside their native range.

Link: https://doi.org/10.3897/neobiota.84.95864.suppl3

Supplementary material 4

Percentages of species native to a region in each feeding guild, regardless of impact. Those in the "Native country: other" category are species native to other regions but not to Australia or New Zealand.

Authors: Eckehard G. Brockerhoff, Belinda A. Gresham, Nicolas Meurisse, Helen F. Nahrung, Anouchka Perret-Gentil, Andrew R. Pugh, Stephanie L. Sopow, Rebecca M. Turner

Data type: figure on feeding guild percentages

Explanation note: supplementary figure on percentages of species native to a region in each feeding guild (borers, defoliators, sap-feeders and others), regardless of impact.

Link: https://doi.org/10.3897/neobiota.84.95864.suppl4